

CHAPTER SIXTEEN

Post-conceptive Mating in
White-Faced Capuchins,
Cebus capucinus:
Hormonal and
Sociosexual Patterns of
Cycling, Noncycling, and
Pregnant Females

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INTRODUCTION

In many species of nonhuman primates, sociosexual behaviors are known to vary across a female's reproductive cycles and thus numerous studies have focused on the relationship between behavior and hormonal fluctuations during the ovarian cycle (e.g., *Macaca fuscata*: Enomoto *et al.*, 1979; *Papio ursinus*: Saayman, 1970; *Erythrocebus patas*: Loy, 1981; *Cebus apella*: Carosi *et al.*, 1999; *Brachyteles arachnoides*: Strier and Ziegler, 1997). Baum (1983) and Beach (1976) have argued that ovarian hormones (i.e., estradiol and progesterone) correlate with aspects of sociosexual behavior such that high levels of estrogen are associated with an increase in proceptive behaviors and female attractiveness, and high levels of progesterone are associated with reduced female proceptivity and female attractiveness. The recent development of non-invasive fecal collection and hormone extraction techniques that can be successfully used in the field have resulted in a growing number of studies that relate hormones to behavior in free ranging primates (*Propithecus verreauxi*: Brockman *et al.*, 1995; *Brachyteles arachnoides*: Strier and Ziegler, 1997; *Macaca nemestrina*: Risler *et al.*, 1987; *Papio cynocephalus*: Wasser *et al.*, 1991).

After reaching sexual maturity, a female primate repeatedly experiences three different reproductive states: ovarian cycling, pregnancy, and anovulation. The period of time when the female experiences fluctuating ovarian hormone levels (i.e., estrogen and progesterone) is known as the "cycling" state. It is during this time that ovulation occurs and a female is able to conceive an infant. The second state, pregnancy, is when the female is carrying a developing fetus. During this period, ovarian hormones remain at elevated levels and help to maintain the fetus throughout gestation. The third state, "anovulation", occurs after parturition in the early phase of lactation. One physiological response of the female primate's body to lactation is the suppression of ovarian function. During anovulation, the hormone fluctuations normally experienced during the "cycling" state do not occur and therefore ovulation and conception cannot occur (Dixon, 1998). Late in lactation, or after the infant is weaned, normal ovarian cycling resumes and the female can conceive another infant. For the purposes of this study, we will refer to females who are not pregnant and not experiencing hormonal cycles as "noncycling." Only a few primate studies have compared the behavioral changes across the different reproductive states (e.g., *Cercocebus torquatus atys*: Gordon *et al.*, 1991; Gust, 1994; *Pan troglodytes*: Wallis, 1982). Our study uses hormone profiles, created from the analysis of

fecal ovarian steroids, to determine the reproductive status of wild female white-faced capuchins, and then examines sexual and affiliative behaviors that are exhibited across the three reproductive states. We have three objectives: (1) to profile the ovarian steroid pattern of female capuchins in different reproductive states, (2) to determine the behavioral indicators from which one could reliably infer the reproductive status of wild female capuchins in the absence of hormonal data, and (3) to explore the reproductive strategies used by wild female capuchins.

Hrdy (1974, 1979) suggested that mating during nonconceptive periods (i.e., when females are either pregnant or anovulatory due to lactation) is a female behavioral counter-strategy to reduce the threat of infanticide by invading males (also see Agrell *et al.*, 1998). Mating during pregnancy (also referred to as “post-conceptive” mating) has been reported in a number of primate species who also experience infanticide (*Cercocebus torquatus atys*: Gordon *et al.*, 1991; *Papio hamadryas*: Zinner and Deschner, 2000; *Pan troglodytes*: Wallis, 1982; also *Cebus capucinus*: Manson *et al.*, 1997). Females of some of these species even go so far as to exhibit “false conceptive signals” that confuse males as to their true reproductive state. For instance, female sooty mangabeys (*Cercocebus torquatus atys*) and hamadryas baboons (*Papio hamadryas*) have been found to display post-conceptive swellings that mimic the swellings experienced during their conceptive periods. However, it was the subordinate sooty mangabey males who mated with the post-conceptive females, while the alpha males mated only with females displaying true conceptive swellings. Thus, the authors inferred that these alpha males were able to discriminate between conceptive and post-conceptive swellings, but they were unable to explain what cues this discrimination was based upon, and why subordinate males chose to mate with pregnant females (Gust, 1994).

Manson *et al.* (1997) examined nonconceptive (pregnant or lactating) mating behavior in white-faced capuchins and found that the pregnant females mated more frequently than the potentially conceptive (cycling) females. In their study, reproductive state was inferred from behavioral observations rather than determined from hormones. The authors concluded that post-conceptive mating in this species functions to confuse paternity among males and reduce the risk of infanticide. To support this theory, Fedigan (2003) and Fedigan and Jack (2004) found that the immigration of new males into white-faced capuchin groups usually occurs through aggressive group takeovers and that these takeovers coincide with the deaths and disappearances of infants.

To the observer, white-faced capuchin females appear inconspicuous in displaying any behavioral or morphological cues that indicate their conceptive phase (i.e., they seem to conceal their ovulation), but adult male capuchin behavior suggests they may be able to recognize this phase in cycling females (Carnegie *et al.*, in press). However, for post-conceptive mating to act as a successful counter-strategy to infanticide, males should not be able to detect the ovulatory phase, and they also should not associate the timing of mating with the timing of births (Zinner and Deschner, 2000). If post-conceptive mating in female white-faced capuchins is a reproductive-strategy, we would expect to see both cycling and pregnant females responding positively to male sexual solicitations by mating with them.

METHODS

Study Site and Species

Our study took place in Santa Rosa National Park (SNRP), Costa Rica (the original sector of the Area de Conservacion Guanacaste, ACG), between the months of January and June, 2002. The park encompasses about 108 km² of dry, deciduous forest which experiences a distinct dry season (mid-December to mid-May) and wet season (late May to early December; average annual rainfall is 1473 mm; Fedigan and Jack, 2001). Data for this project were collected during the dry season because most trees lose their leaves and the increased visibility makes it easier to follow individuals and collect fecal samples. The white-faced capuchins (*C. capucinus*) in SRNP live sympatrically with two other species of nonhuman primates; *Alouatta palliata* (mantled howling monkey) and *Ateles geoffroyi* (black handed spider monkey).

White-faced capuchins live in multimale/multifemale social groups that consist of related females, immigrant males, and immature offspring. White-faced capuchins engage in sexual behavior (copulations and solicitations) throughout the year but we have found a birth peak between January and April (Fedigan, 2003). Females become reproductively mature (i.e., start ovarian cycling) around the age of 5 years and the first age of first birth in this population is between 6 and 7 years. Females do not show any conspicuous signs of ovulation (i.e., no morphological changes and overt behavioral changes; Carnegie *et al.*, in press). There is a discernable linear hierarchy within a group of capuchins and

Table 1. Group, age, rank, reproductive state, and history for each female in 2002

Female	Group	Age ^a	Rank	Reproductive state	Parity	Age of last infant ^b
Limp	CP	24	Alpha	Cycling	Multiparous	12
Kathy Lee	LV	13	Alpha	Cycling	Multiparous	12
Blanquita	LV	20	Subordinate	Cycling	Multiparous	9
Timone	CP	6	Subordinate	Cycling	Nulliparous	0
Nyla	CP	8	High rank	Noncycle	Multiparous	12
Seria	CP	13	Subordinate	Noncycle	Multiparous	7
Fiesty	LV	20	Subordinate	Noncycle	Multiparous	9
Pumba	CP	8	Subordinate	Pregnant	Multiparous	24
Dos Leches	LV	11	High rank	Pregnant	Multiparous	12 ^c
Salsa	LV	6	Subordinate	Pregnant	Nulliparous ^d	0

^a Age of female in years.

^b Age of infant in months from parturition to January 2002.

^c This female lost her last infant (disappeared) less than 1 month after it was born resulting in a shorter interbirth interval.

^d This female gave birth to her first infant during the study (May 2002).

within the sexes (Perry, 1997). One male is usually dominant over the others but not to the point of exclusive access to females, as is commonly seen in *C. apella* or *C. olivaceus* (Janson, 1984; Robinson, 1988; Fragaszy *et al.*, 2004).

The subjects for this study consisted of 10 wild adult female white-faced capuchins that were part of two habituated groups; Cerco de Piedra and Los Valles (5 per group). Females ranged in age from 6 to ~24 years. Additionally, there were six adult males: two alpha males and four subordinate males. Individuals were identified by natural markings such as broken digits, scars, hair coloring, and the brow and peak shape. This population of capuchins has been under study by LMF's research team since 1983. Capuchins are female bonded (Fragaszy *et al.*, 2004), and kinship relations among females are known for the last 15–20 years. Table 1 lists information on the group, rank, and reproductive history for each of the 10 females.

Behavioral and Fecal Data Collection and Analysis

Between January and June, 2002, we collected 443 h of focal animal data (ranging from 39 to 47 h per female) between 6 am and 6 pm. Focal sessions lasted for 15 min each, during which time all behaviors and interactions were recorded continuously (Altmann, 1974). We used hand-held computers (PSION

Workabout MX) and entered data into a software program entitled “Behavior”, which was designed by Syscan International Inc. (Montreal, Quebec) for our use. We employed an exhaustive ethogram developed over the years by previous *C. capucinus* researchers to identify and code behaviors.

We collected fecal samples from each focal female on every day that behavioral collection occurred. A minimum of two to three samples per week per female were enough to assess ovarian patterns in females but additional samples were collected in case females could not be located in subsequent days (Hodges and Heistermann, 2003). After the pregnant females gave birth, we collected only one sample per week per female which was sufficient to monitor post-partum ovarian function. In total, we collected 600 samples from the 10 subject females. Fecal collection and initial extraction of the steroids in the field followed the techniques described in Strier and Ziegler (1997) and Strier *et al.* (2003). The samples were refrigerated until transported to the National Primate Research Center (NPRC, University of Wisconsin) in Madison for the laboratory analysis.

We conducted the hormone assays at the NPRC (University of Wisconsin) during July and August 2002. Before these analyses, the third author validated 10 previously collected fecal samples in January 2001 for estradiol and progesterone and the enzyme-immunoassays and radio-immunoassays that were used to assess those hormones, respectively. Before assays were performed, it was necessary to perform solvolysis to break conjugated steroids into unconjugated forms. This procedure has been previously described in Ziegler *et al.* (1996) and Strier *et al.* (1999).

We used the results of the fecal assays to create hormone profiles for each adult female and from the profiles we were able to categorize females as being in one of the three reproductive states: cycling, noncycling, or pregnancy. We identified noncycling females by nonfluctuating and sustained baseline levels of estradiol and progesterone. The gestational period of pregnant females was identified by elevated levels of both steroid hormones, which drop drastically to baseline levels after parturition. Cycling females were identified by fluctuating levels of estradiol and progesterone which are representative of the periovulatory and non-ovulatory phases of the ovarian cycle (Dixson, 1998; Carnegie *et al.*, submitted).

For unknown reasons, four of the females whom we classified as “cycling” actually stopped cycling mid-way through the study (e.g., they did not become pregnant). Therefore, for this analysis, we used only behavioral data collected

from them while they were cycling (cycling: 55.25 h). We analyzed behavioral data collected from the pregnant females ($N = 3$) only while they were pregnant and not after they gave birth (68.75 h). For consistency, we analyzed behavioral data collected from the noncycling females ($N = 3$) between January 15 and April 30 (68.5 h). We choose the later date because most of the cycling females had stopped cycling at this time and there was only one pregnant female still to give birth (her parturition date was May 13).

The behavioral variables analyzed for reproductive state variation were: urine washing (rubbing urine into the hands and feet), copulations and courtship displays (sexual behavior), and the hypothesized behavioral indicators of attractiveness, proceptivity, and receptivity. For proceptivity indicators, we used grooming (frequency of groom solicits and frequency and duration of grooming bouts) *directed* by the subject female to adult males. We considered the same behaviors as indicators of attractiveness when they were *received* from adult males. We measured receptivity as a percentage of male courtship displays to which females responded positively by presenting for mounting and facilitating copulations.

We compared each of the behavioral frequencies across each category of females (noncycling, cycling, and pregnant) by calculating a mean rate (frequency per hour) for each of the subject females for each reproductive state. We determined mean grooming duration by tallying the total amount of time females spent in grooming bouts and calculating the proportion of that time they spent grooming (or spent being groomed by) adult males.

We used Hinde's Index (Hinde and Atkinson, 1970) to decide which member of the male–female dyad was responsible for maintaining proximity. Hinde's Index is the proportion of all of the dyad's *approaches* directed by the subject female, minus the proportion of all of the dyad's *leaves* directed by the female. A negative index indicates that the male was responsible for maintaining proximity; a positive index suggests that the female was responsible. *Approaches* to within 3 m and *leaves* beyond 3 m were used in this analysis.

We used Kruskal–Wallis one-way analysis of variance (nonparametric test) to compare behavioral frequencies among reproductive states (Siegel and Castellan, 1988; Zar, 1999). All frequencies showing a significant difference were further analyzed using a multiple comparison test to determine where the difference existed among the three categories of females (Siegel and Castellan, 1988).

RESULTS

Hormone Validations and Profiles

Mean steroid recoveries were within acceptable values for progesterone (90.7%) and estradiol (64.5%; recoveries should normally be greater than 75%, but E2 recoveries were consistent over all eight assays so this value was accepted). Pooled samples compared for accuracy and parallelism to the standard curve were high for both progesterone (P) and estradiol (E2) assays (>100% accuracy; accepted values are between 80% and 120%; slopes did not differ statistically). Additionally, mean intra-assay coefficient of variations (CV) were 6.89% for P and 4.73% for E2 (acceptable values are less than 10%). Inter-assay CV values were 8.56% for P and 8.20% for E2 (acceptable values are less than 20%).

The hormone profiles created from the fecal analysis clearly revealed that three females were noncycling for the duration of the study, three females were pregnant at the beginning of the study (and subsequently gave birth during the study), and four females displayed regular cycling for a period of time and then stopped mid-way through the study period without becoming pregnant (cycling females). Figures 1a, 1b, and 1c illustrate representative hormone profiles for noncycling, cycling, and pregnant females, respectively.

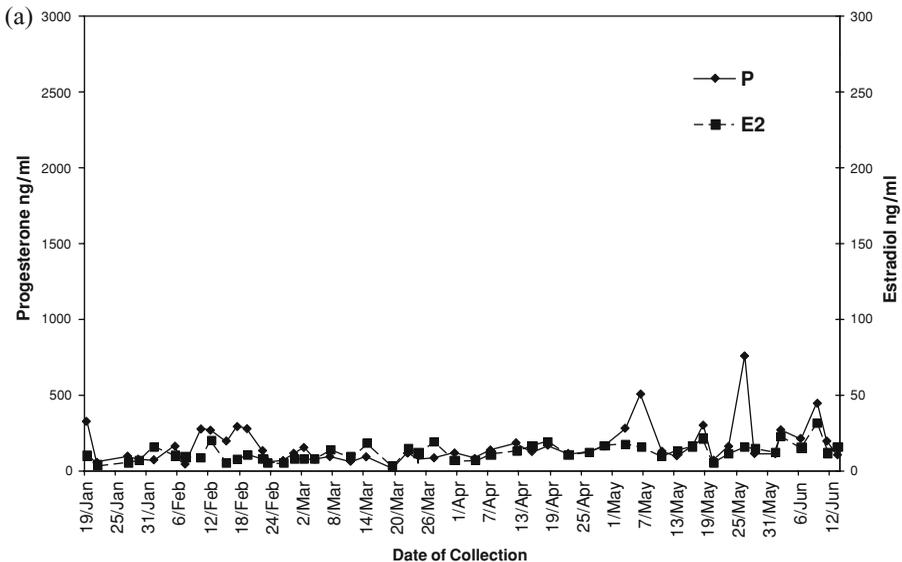


Figure 1. (a) Representative hormone profile for one noncycling female white-faced capuchin. Estradiol (E2) and progesterone (P) remained near baseline levels for the entire duration of the study; (*Continued*)

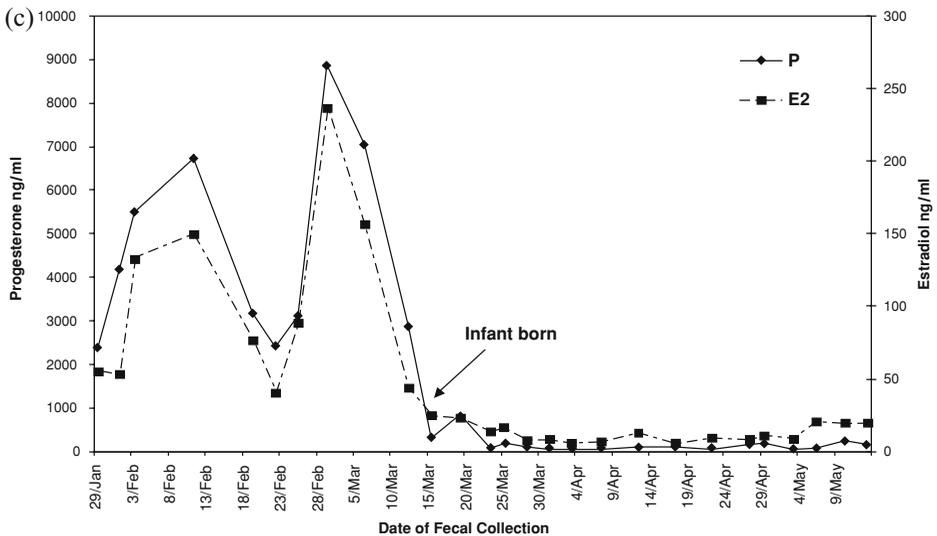
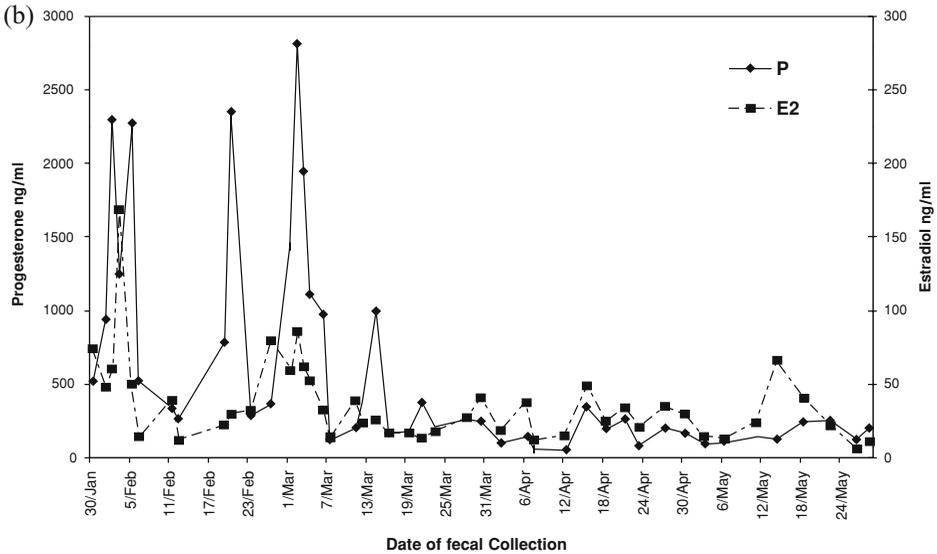


Figure 1. (Continued) (b) representative hormone profile for one cycling female white-faced capuchin. This female appeared to have already started cycling when observations commenced and displayed two cycles before she stopped in early March; and (c) representative hormone profile for one pregnant female white-faced capuchin. Pregnancy is represented by elevated progesterone (P) and estradiol (E2) which drop to baseline levels 1–2 days after parturition. The date of parturition is labeled (March 14).

Table 2. Summary of the ovarian hormone patterns for the cycling females

Female	Group	Length of complete cycle 1/cycle 2 (days) ^a	Length of total cycling period (days) ^b	Date of cycling cessation	Length of noncycling period (days) ^c	Length of time since last infant born (months) ^d
TI	CP	25/-	47	March 19	86	0
LI	CP	22/-	41	April 12	62	12
KL	LV	26/-	48	March 16	73	12
BL	LV	14/13	38	April 18	40	9

^a A complete cycle was calculated from one progesterone surge to the next.

^b The length of the cycling period was calculated from the first day of the P surge to the end of the cycling when P levels decreased and did not rise again.

^c The length of the noncycling period was calculated from the date of cycling cessation to the date the last sample was collected.

^d This population of capuchins have a 2.5-year interbirth interval (Fedigan, 2003); gestation lengths are approximately 5.5 months (Nagle and Denari, 1982).

Of the four cycling females, three did not show cycling until 14, 41, and 43 days after their first collected sample. Our observations on the fourth female appeared to start at the beginning of her luteal phase. This phase is characterized by elevated levels of E2 and P that are produced by the *corpus luteum*, which is formed from the follicle after ovulation. The onset of cycling was indicated by the abrupt rise in the concentrations of progesterone and estradiol from near baseline levels. Regular cycling for all females ceased when both steroid hormones dropped to near baseline and did not elevate again to the previous (ovulatory) levels. We calculated between one and three regular cycles for each female during observations that extended over an average of 43.5 days (range: 40–86 days). Table 2 summarizes the ovarian hormone patterns for each of the cycling females.

Behavioral Variation Among Noncycling, Cycling, and Pregnant Females

Sexual Behavior

We found significant differences in the rates of copulations and courtship displays across the three reproductive states (copulations: $\chi^2 = 7.52$, $df = 2$, and $p = 0.023$; courtship displays: $\chi^2 = 7.891$, $df = 2$, and $p = 0.019$). Multiple comparison tests revealed that pregnant females copulated and received more courtship displays from all adult males than did cycling females (Figure 2).

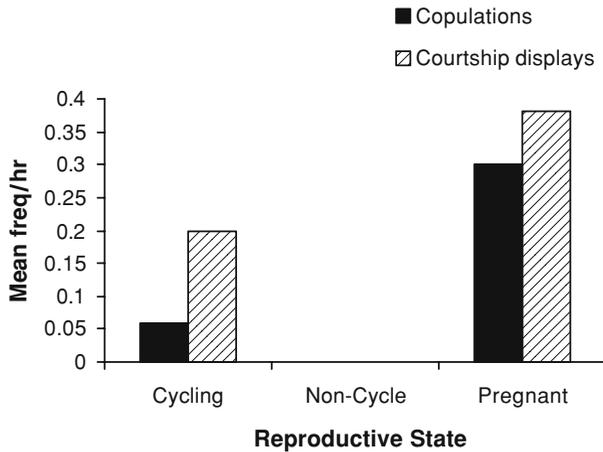


Figure 2. Mean rate of copulations with adult males and the mean rate of courtship displays (sexual solicitations) that cycling, noncycling, and pregnant females received from adult males.

Noncycling females were never observed to copulate with, or receive a courtship display from, an adult male.

In total, there were 22 copulations observed and 19 of these involved pregnant females mating with subordinate males. There were 32 courtship displays observed and 21 of these involved pregnant females—19 of which came from subordinate males. Additionally, pregnant females responded positively to 100% of the courtship displays they received from subordinate males (19 displays) by presenting for and facilitating copulation, whereas they never responded positively to any of the alpha males' solicitations (three displays). Furthermore, one and two days, respectively, *after* giving birth, two of the “pregnant” females copulated once each with a subordinate male.

The remaining three copulations occurred between cycling females and adult males two of which were with alpha males. Cycling females received the remaining 11 courtship displays and 8 of these were from the alpha males (73%). Cycling females responded positively to only 3 of the 11 courtship displays directed to them (27%).

Proceptivity

The rate of *grooming bouts directed to subordinate males* by subject females varied significantly across states ($\chi^2 = 6.85$, $df = 2$, and $p = 0.033$). Multiple

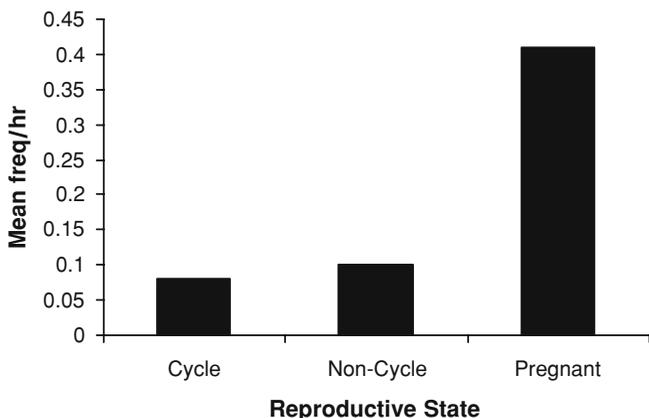


Figure 3. Mean rate of grooming bouts directed to subordinate males by cycling, noncycling, and pregnant females.

comparison tests revealed that pregnant females directed grooming bouts to subordinate males at a significantly higher rate (0.41/h) than did cycling (0.08/h) and noncycling females (0.10/h) (Figure 3).

Attractivity

The rates of *grooming bouts* and *groom solicits received from alpha males* by subject females varied significantly across reproductive states (grooming bouts; $\chi^2 = 7.63$, $df = 2$, $p = 0.02$; groom solicits: $\chi^2 = 6.82$, $df = 2$, $p = 0.032$). Multiple comparison tests show that cycling females received grooming bouts from alpha males at a significantly higher rate (0.13/h) than did either the pregnant (0.02/h) or the noncycling females (none) (Figure 4a). Cycling females received solicitations to be groomed from alpha males at a higher rate (0.22/h) than did the noncycling females (0.01/h) but the rate was comparable to pregnant females (0.15/h) (Figure 4b).

Proximity

Hinde's index was calculated to determine which sex was responsible for maintaining proximity in the male–female dyads (Table 3). In the “cycling female” category, only 10 out of a possible 12 dyads could be calculated as 1 male was never within proximity to subject females. All four dyads involving the alpha males were negative, which implies the alpha males were responsible for

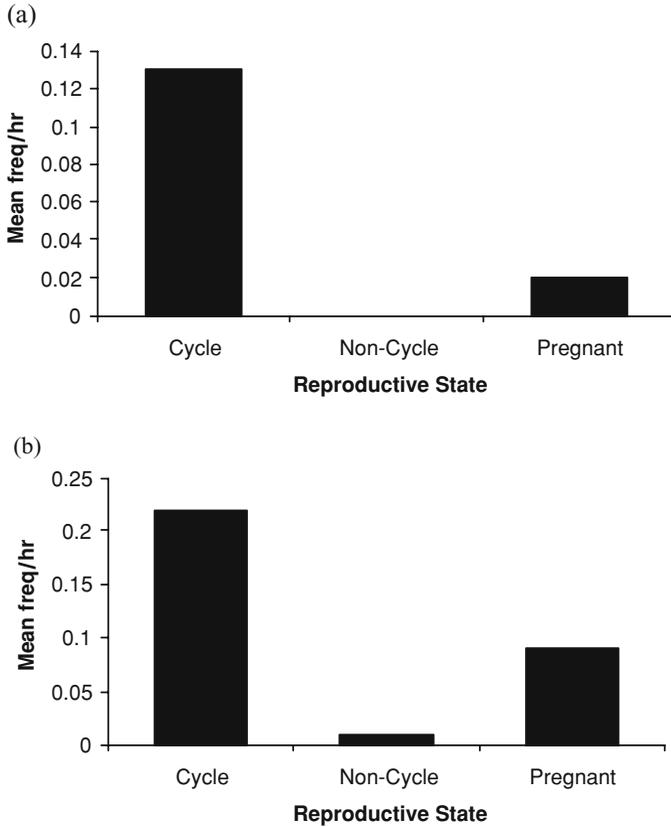


Figure 4. (a) Mean rate of grooming bouts that cycling, noncycling, and pregnant females received from alpha males and (b) mean rate of groom solicits that cycling, noncycling, and pregnant females received from alpha males.

Table 3. Percentage of dyads for which either the male or the female maintained proximity in each reproductive state. Values calculated using Hinde’s Index

	Cycling	Noncycling	Pregnant
Male maintained			
Alpha	100	0	67
Subordinate	67	100	80
Female maintained			
Alpha	0	100	33
Subordinate	0	0	0
Neutral	33	0	20

maintaining proximity 100% of the time with cycling females. Four of the six dyads involving the subordinate males were negative (67%) and the two remaining dyads were neutral (33%), which implies that there was no difference between the sexes in who maintained the proximity.

In the pregnant female category, 8 out of a possible 10 dyads could be calculated. Two of the three dyads involving the alpha males were negative (67%) and one was positive (33%), which implies the pregnant female was responsible for maintaining proximity in that dyad. Of the five dyads involving the subordinate males, four were negative (80%), and the remaining dyad was neutral (20%).

Among noncycling females, 8 out of the possible 10 dyads could be calculated. In contrast to the other females, all three of the dyads involving the alpha males were positive (100%) which implies that the noncycling females were entirely responsible for maintaining proximity with the alpha males. In contrast, all five of the dyads involving the subordinate males were negative (100%).

Urine Washing

We found a significant difference in the rate of urine washing between cycling, noncycling, and pregnant females ($\chi^2 = 6.56$, $df = 2$, and $p = 0.03$). Cycling females performed urine washes at a significantly higher rate (3.12/h) compared to both pregnant (1.54/h) and noncycling females (1.67/h) (Figure 5).

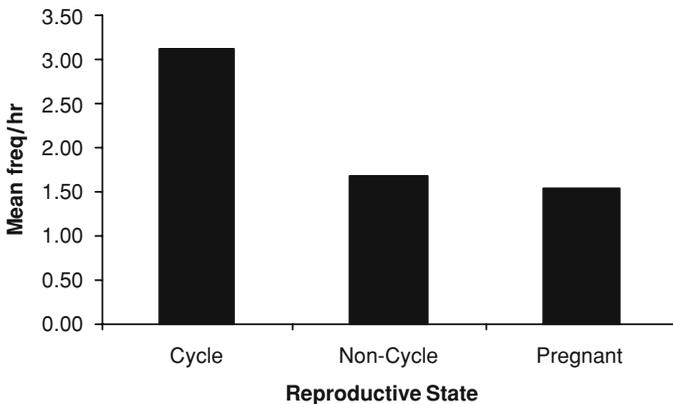


Figure 5. Mean rate of urine washing displayed by cycling, noncycling, and pregnant females.

DISCUSSION

Fecal Hormone Analysis and Interpretation of Hormone Profiles

The results from the hormone assays revealed that the collection and extraction techniques used in the field and the laboratory were successful methods for studying ovarian steroids in white-faced capuchin feces. Noncycling, cycling, and pregnant females were easily recognized from the hormone profiles created from the fecal analysis.

The three noncycling females were identified by their sustained baseline levels of estradiol and progesterone that lasted throughout the study. We could confirm that the pregnant females were in fact pregnant by their hormone profiles (characteristic elevated levels of ovarian hormones during gestation, which dropped to baseline after parturition), their expanding bellies, and the fact that they all gave birth during the study. We were not able to calculate gestation lengths as all three females were already pregnant when we began in January 2002. However, we assume that white-faced capuchins have gestation lengths similar to *C. apella*, of 22–23 weeks (Nagle and Denari, 1982), therefore, these females probably conceived between October and December of 2001.

The four cycling females stopped cycling between March and April (2002) after each experiencing one to three cycles, even though pregnancy had not been achieved. After the cycles stopped, hormone levels stayed low and fluctuated slightly but never reached or sustained baseline levels compared to the noncycling females (see Figure 1b). It is unclear why these four females stopped cycling and did not get pregnant. The following year (2003), all four of these females gave birth between the months of February and May; therefore, they must have started to cycle again and conceived between September and December, 2002 (assuming a 5.5-month gestation period; Nagle and Denari, 1982). Further studies on this cessation and resumption of cycling are presently being conducted.

Behavioral Indicators of Reproductive State

Our original prediction that cycling and pregnant females would be involved in sexual and social behaviors at higher rates than noncycling females is supported by our findings in this study. In fact, one of our most interesting findings is that pregnant females mated more often than any of the other females and they

did so almost always with subordinate males. Furthermore, the cycling females mated only with the alpha males, and did not mate with any subordinate males, even though they were solicited by them. Pregnant females received significantly more sexual solicitations from subordinate males and were over three times more likely to respond positively to solicitations from males compared to the cycling females. Moreover, alpha males directed courtship displays toward cycling females at three times the rate they directed them to pregnant females.

We also found that proceptive and attractive behaviors involved cycling and pregnant females at much higher rates compared to the noncycling females. Specifically, the rate of grooming bouts that pregnant females directed toward subordinate males was much higher than grooming directed by cycling or noncycling females. Additionally, cycling females received groom solicits and grooming bouts from alpha males at the highest rate. We found that alpha males maintained proximity to cycling females, and subordinate males maintained proximity to pregnant females more than to any other category of female (i.e., cycling or noncycling). In contrast, we also found that noncycling females were responsible for maintaining proximity to the alpha males in all cases.

One exception to our predictions was that noncycling females maintained a close proximity to the alpha males (suggesting proceptivity). Among the three noncycling females, only one was very high ranking and the other two were low ranking and often remained on the outskirts of the group; therefore, it is possible that the two females were trying to maintain a close proximity to the alpha males in an effort to associate with high ranking individuals. By staying close to the alpha male, and therefore more central within the group, they might have had better access to resources or benefit from greater group protection in case of an inter-group encounter or predator attack.

Reproductive Strategies in White-Faced Capuchins

In light of our findings on sexual behavior in this species, two questions are raised concerning male and female mating strategies: (1) why do subordinate males court pregnant females more often than they do cycling females? and (2) why did pregnant females mate with subordinate males as often as they did, and not with the alpha males, even after they were solicited by the latter?

One explanation for mating behavior between pregnant females and subordinate males may be related to the elevated levels of stimulating estrogen that

pregnant females produce during gestation; in that high estrogen levels may influence males to be more attracted to pregnant females and females to be more proceptive to males (Beach, 1976; Baum, 1983). However, if this were the case, we would expect the alpha males to be just as attracted to the pregnant females as were the subordinate males.

Gordon *et al.* (1991) and Gust (1994) found that alpha male sooty mangabeys (*Cercocebus torquatus atys*) discriminate between a female's fertile and nonfertile or post-conceptive swellings. The researchers found that alpha males only mated with females during their fertile swellings and never mated with pregnant females, whereas subordinate males mated with pregnant females during their nonfertile swelling phases. They found no difference in the concentrations of estradiol or progesterone between the two types of swellings, but the concentration of lutenizing hormone (LH) was significantly higher in the fertile females. The implication is that alpha males may be sensitive to the olfactory cues of the differing LH concentrations between the two groups of females, which helps them to discriminate between a conceptive and nonconceptive female. There is some evidence to support the notion that LH stimulates sexual behavior in male rats and male primates; however, it is inconclusive and more research is still needed (see Dixson, 1998).

Urine washing occurs in many primate species including squirrel monkeys, woolly spider monkeys, and all species of capuchins (Boinski, 1992; Milton, 1985; Robinson, 1979). Urine washing has been suggested to function as an olfactory indicator of reproductive status (Boinski, 1992; Perret, 1992), and it may act as a non-affiliative proceptive behavior. Often, we see male white-faced capuchins smelling and licking branches where a female has performed a urine wash. Previously (Carnegie *et al.*, in press), we demonstrated that urine washing was not related to ovarian phase (i.e., periovulatory versus non-ovulatory), and in the present study, we found that urine washing occurred at significantly higher rates among the cycling females compared to the noncycling and pregnant females. Therefore, in this species, olfaction may play a role in communicating reproductive state rather than ovarian phase. The use of olfaction by anthropoid primates is not as well studied as it is in prosimians (Schilling, 1979) and further studies need to be done to understand how olfaction is used in cebids and other anthropoids.

It is unclear why subordinate males would sexually solicit pregnant females when there is no obvious reproductive advantage to this behavior. Gust (1994)

could not conclude that hormonal differences in female sooty mangabeys accounted for the behavioral differences observed between the alphas and subordinate males. Nevertheless, if alpha males are able to discriminate between LH concentrations in cycling and pregnant females, it is more than likely that subordinate males can do the same. Therefore, it is possible that from the subordinate males' perspective, post-conceptive mating has little or nothing to do with increasing reproductive fitness but instead functions to build social bonds and increase sexual familiarity and/or reduce inter-sexual tension (Gust, 1994; Manson *et al.*, 1997).

As to our second question, pregnant females may choose to mate with subordinate males in order to confuse the male as to the paternity of the soon-to-be-born infant (Hrdy, 1974, 1979). Infanticide does occur in this species and it is often carried out by immigrating and/or lower ranked males after a rank reversal (Fedigan, 2003). It is argued that in forming a sociosexual bond with the mother, subordinate males are less likely to harm a newborn and instead will stay in the group to help protect the infant from predators and invading males (Hrdy, 1974; Agrell *et al.*, 1998; Fedigan, 2003).

Previously, we have found that these capuchin females mate more often with the alpha males during their conceptive phase (two out of three copulations), and paternity studies have shown that the alpha males sire almost all of the infants within their groups (Jack and Fedigan, this volume; Jack and Fedigan, 2003). Therefore, it can be assumed that the pregnant females have already mated and conceived infants with the alpha male during their regular ovarian cycling period. Since lower ranked (and immigrating) males may pose a high risk to a new infant in terms of infanticide, by being receptive to the male's solicitations during gestation and even within days of parturition, the pregnant female may be forming a positive bond with a male, thereby reducing the likelihood of aggressive encounters with him once the infant is born.

Forming and maintaining strong social bonds could also be facilitated through grooming. Our finding that the pregnant females were grooming the subordinate males more often than the alpha males supports the theory that the pregnant females are trying to form positive bonds with males that could potentially harm their infant in the event of a rank reversal. Moreover, formation of these bonds may also facilitate a protective relationship and, in the case of an extra group male takeover, these subordinate males may help protect the female and her new infant. Additionally, the close proximity that is required for grooming means that the female is accessible to that male for mating.

However, for these strategies to be successful, males must not be able to associate the timing of mating with the timing of births (Zinner and Deschner, 2000).

SUMMARY

In many primate species, sociosexual behaviors are known to vary throughout a female's reproductive cycle, yet few studies have focused on changes in behavior across reproductive states. We examined sexual and affiliative behaviors that are exhibited across three reproductive states: cycling, noncycling, and pregnancy, in wild white-faced capuchins. To reliably determine reproductive state, we analyzed fecal steroids to create hormone profiles for each of the subject females. Our objectives were to determine the behavioral indicators from which one could reliably infer the reproductive status of wild female capuchins in the absence of hormonal data, and in doing so, to explore the reproductive strategies used by female capuchins.

Our hormonal analysis was successful and revealed some interesting aspects of female capuchin reproduction. We found that the cycling females stopped cycling mid-way through the study but did not become pregnant. We are uncertain as to why they stopped cycling and further research into this finding is presently underway. We found that cycling and pregnant females copulated and received more courtship displays from adult males than did noncycling females. Sexual behaviors were more commonly seen between pregnant females and subordinate males, and between cycling females and alpha males. Pregnant females displayed proceptive behaviors at higher rates toward subordinate males, and cycling females received attractivity indicators at higher rates from alpha males. Noncycling females were rarely, if at all, involved in sexual, proceptive, or attractive behavioral indicators. However, they were responsible for maintaining close proximity to the alpha males 100% of the time. Finally, we found that urine washing occurred at higher rates among the cycling females compared to the other females.

We conclude that the high rate of sexual behavior and proceptivity between the pregnant females and the subordinate males may be associated with a female-strategy to prevent infanticide. By mating with lower ranked males and by forming positive bonds with them, pregnant females confuse males as to the paternity of the new infant and encourage them to be protective in the eventuality of an aggressive male take-over.

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